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Associations Between Egg Capsule Morphology and Predation Among Populations of the Marine Gastropod, *Nucella emarginata*

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Abstract. Intraspecific variation in the morphology of egg capsules is ideal for assessing the costs and benefits of encapsulation, yet little is known about the extent of such variation among populations of a single species. In the present study, I compared capsule morphology among three populations of the intertidal gastropod, *Nucella emarginata*. Significant differences were found both in capsule wall thickness and capsule strength. Mean capsule wall thickness varied as much as 25% among populations, with the dry weight of capsular cases differing accordingly. Capsule strength, measured as resistance to puncturing and squeezing forces, also varied among populations, but did not directly reflect differences in capsule wall thickness. Despite extensive variation in capsule morphology within this species, the number and size of eggs contained within capsules of equal volume did not differ significantly among populations.

I also compared the type of capsule-eating predators that were present at each site. Shore crabs, *Hemigrapsus* spp., were abundant at all three sites; however, the predatory isopods *Idotea wosnesenskii* were only present at sites containing relatively thick-walled capsules. Although *Hemigrapsus* and *Idotea* were able to chew through both thick- and thin-walled capsules, laboratory experiments revealed that *Idotea* preferentially opened thin-walled capsules. These results suggest that variation in capsule morphology among populations of *N. emarginata* may, at least in part, reflect selection for the protection of embryos against predation.

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Introduction

The confinement of developing embryos within elaborate egg capsules is a common phenomenon among marine invertebrates. Although this trait is widespread, few studies have addressed the benefits and costs associated with the production of encapsulating structures. Egg capsules may protect embryos from such environmental stresses as: predation (Pechenik, 1979; Perron, 1981), bacterial attack (Lord, 1986), osmotic changes (Pechenik, 1982, 1983; Hawkins and Hutchinson, 1988), desiccation (Spight, 1977; Pechenik, 1978), temperature shock (Spight, 1977; Pechenik, 1986), and wave action (Perron, 1981). Yet the ability of capsule walls to resist such stresses is known for only a few species (Emlen, 1966; Spight, 1977; Pechenik, 1978; 1982; 1983; Brenchley, 1982; Lord, 1986; Hawkins and Hutchinson, 1988), and only limited data are available on the survivorship of encapsulated embryos in the field (Spight, 1977; Pechenik, 1978; Brenchley, 1982). The production of egg capsules must also have associated costs. Capsule walls can divert a substantial amount of energy away from the production of eggs (Perron, 1981) and may also limit the availability of oxygen and nutrients to encapsulated embryos (Strathmann and Chaffee, 1984). If the adaptive significance of encapsulation is to be understood, these benefits and costs must be assessed.

Encapsulation of developing embryos is widespread among the more advanced gastropods (Pechenik, 1986). Neogastropod mollusks enclose embryos within structurally complex proteinaceous capsules and attach these structures to firm substrata in the marine environment. Within this group, egg capsule morphology varies tremendously (*e.g.*, Ostergaard, 1950; D'Asaro, 1970, 1988; Perron, 1981). Subtle differences in the properties of these

capsules may reflect tradeoffs between benefits and costs of encapsulation (Perron, 1981; Perron and Corpuz, 1982). For instance, Perron (1981) found that capsule wall strength, and the proportion of reproductive energy invested in capsular cases, varied among closely related species of *Conus*. These differences were directly related to the development time of encapsulated embryos, such that embryos with long-term development were enclosed in thicker, stronger, and energetically more expensive capsules than those with short-term development (Perron, 1981; Perron and Corpuz, 1982). Thus, energetic costs associated with the production of strong capsular cases may be compensated for by the benefits of increased embryonic protection in species with protracted intracapsular development.

If variation in the morphology of egg capsules does reflect tradeoffs associated with specific benefits and costs of encapsulation, then intraspecific variation in capsular structure offers an ideal opportunity to assess such benefits and costs. Unlike interspecific comparisons, which may be subject to potentially confounding phylogenetic effects, studies of variation within a species can determine the importance of (1) physical constraints in female body size, (2) phenotypic responses to variation in environmental conditions and, (3) genetic divergence resulting from selection, in accounting for differences in capsule morphology. In no studies, however, have the structures of egg capsules in different populations of a single species been compared, and little is known about the extent of intraspecific variation in capsule morphology.

The widespread geographic distribution and direct development of the marine intertidal snail *Nucella emarginata* (Deshayes, 1839) (Prosobranchia: Muricidae) make this species an ideal candidate for studies of intraspecific variation in capsule morphology. These snails are common inhabitants of rocky shores from California to Alaska and range across wide extremes in wave exposure. *N. emarginata* deposit eggs year-round within 6–10 mm-long vase-shaped capsules and attach these structures directly to the substratum. After approximately 80 days of encapsulation (Emlen, 1966), embryos emerge as juvenile snails. Due to the absence of a planktonic larval stage in this species, gene flow among geographically separated habitats may be low (Palmer, 1984). As a consequence, snail populations may have become adapted to localized environmental conditions.

In this study, I examined variation in capsule morphology among three populations of *N. emarginata* separated along a gradient of wave-exposure. I compared capsule size, protective quality (as determined by wall thickness and capsule strength measurements), and capsule contents, among these study populations. Intraspecific differences in capsule morphology were examined with respect to site differences in the presence and abundance of capsule-eating predators. Previous studies, such as those by Emlen (1966) and Spight (1977), have indicated that predation on encapsulated *Nucella* embryos can be severe.

Materials and Methods

Study sites

This study was conducted at the Bamfield Marine Station on the west coast of Vancouver Island, British Columbia. Three study sites were established in Barkley Sound along a gradient of wave-exposure from sheltered to exposed: Grappler Inlet (48°49′N, 125°07′W), Ross Islets (48°52′N, 125°09′W), and Seppings Island (48°50′N, 125°12′W). Although no empirical studies have ranked these areas with respect to wave-exposure, my rating system, based on visual observations, corresponded with exposure scales used by others in the same geographic region (Austin *et al.*, 1971; Kitching, 1976; Craik, 1980; Crothers, 1984).

Intraspecific variation in capsule morphology

Snail size and capsule size. To compare the size of capsules produced by snails from each site, I collected 100 snails from each study area in March 1988. Collections were made by removing all living *Nucella emarginata* individuals from a given area, except for snails smaller than 10 mm in length, which were considered to be reproductively immature. Snails were brought into the laboratory, measured for shell length (apex to tip of siphonal canal) with Vernier calipers, tagged for identification, and then placed in mesh-panelled plastic containers (32 × 26 × 12 cm). Approximately 40–50 snails were held in each container and provided with barnacles (*Balanus glandula*) for food. Containers were kept submerged in seawater tanks and supplied with a continuous flow of fresh seawater. A snail was recognized to be laying an egg capsule only if it was found molding a new capsule with its ventral pedal gland. Other capsules were considered to be part of the same clutch if they were laid within a few millimeters of the freshly spawned capsule and were similar in shape and orientation (see Gallardo, 1979). Five capsules were collected from each female, and then preserved in 5% formalin (in seawater) for subsequent measurement. Egg capsule proteins are known to be stable in this fixative (Hunt, 1971).

I recorded the total capsule length, chamber length, and chamber width for each egg capsule. Total capsule length was the length of the capsule including the plug, but excluding the stalk, as the stalk length was known to be highly variable (Spight and Emlen, 1976). Chamber length and chamber width were measures of the maximum dimensions of the region housing developing embryos and

nutritive nurse eggs. The volume of the capsule chamber was estimated from these measures using the formula for a prolate ellipsoid, $V = 4/3\pi(a/2)(b/2)^2$, where a = chamber length and b = chamber width (Pechenik, 1982).

Micromorphology of N. emarginata *egg capsules.* To examine the microstructure of *N. emarginata* capsules from each site, representative capsules were collected from field populations and then sectioned (unfixed) along sagittal and transverse planes using a freeze microtome. The wall microstructure of these sections was viewed under a compound light microscope and interpreted with reference to previous histological studies of the egg capsules of *N. lapillus* and other muricids (Bayne, 1968; Tamarin and Carriker, 1967; Sullivan and Maugel, 1984; D'Asaro, 1988).

The thickness of capsule walls was examined by taking serial cross-sections down the length of the chamber. Capsules were always selected from separate clutches to ensure that at least some were laid by different snails. Representative capsules were then measured, emptied of all contents by removing the capsular plug, and individually frozen on a freeze microtome. One section (10–12 μm thick) was taken at 10 percentile intervals along the length of the capsule chamber, starting at the opening of the plug region into the capsule chamber (0%) and ending at the base of the capsule chamber (100%). Sections were mounted in a seawater-soluble medium and then measured using a compound microscope with a calibrated ocular micrometer. Eight measurements of wall thickness were taken at approximately equal intervals around the circumference of each capsule section. The average wall thickness within each section was used in all subsequent data analyses.

To examine wall thickness differences among a large number of egg capsules, I established a laboratory population of 60 snails (30 males; 30 females) from each site. For each population, five male and five female snails were allocated to one of six replicate mesh-panelled plastic containers (26 × 16.5 × 13 cm), and were maintained in the laboratory as described above. Every two weeks, freshly laid capsules were collected from each container and placed in small mesh-panelled vials. Vials were then labelled, dated, and immersed in flowing seawater. Capsules required for experiments were selected by removing an equal number (whenever possible) from each replicate vial. Only relatively fresh capsules (within 4-weeks after deposition) were used in the following experiments, since capsule wall properties may change with age (see Roller and Stickle, 1988).

To examine variation in capsule wall thickness within and among populations of *N. emarginata*, 30 capsules were selected from each laboratory population. Each capsule was marked at a point 70% along the length of the capsule chamber. Preliminary data on wall thickness variation within a capsule indicated that capsule walls were thinnest and least variable in this region. For subsequent measurement, capsules were frozen on a freeze microtome and then sectioned at the marked region.

In addition, I examined variation in capsule wall thickness within and among clutches to determine whether females from the same population produced capsules of a similar wall thickness. For each laboratory population, egg capsules were collected from five different females by removing one clutch of capsules from each replicate container. Depending on clutch size, four to six capsules were selected from each clutch and then sectioned as described above.

To determine whether intraspecific variation in capsule wall thickness resulted in differences in the total amount of material allocated to capsular cases, I compared the dry weights of capsular cases from each site. Representative capsules were collected from each laboratory population, measured, and emptied of all contents. Stalks were removed from capsules to minimize variability in weight among capsules. Capsules were rinsed twice in distilled water, dried for 48 h at 75°C, and then weighed to 0.01 mg.

Capsule wall strength. I used two indices to measure the strength of egg capsule walls. The first index determined the resistance of capsule walls to puncturing forces and was based on Perron's (1981) procedure for *Conus* egg capsules. Freshly laid capsules were collected from laboratory populations and marked at a point 70% along the length of the capsule chamber. Capsules were then bisected by cutting along the two seams of the capsule chamber. Each capsule half was mounted individually between two pieces of Plexiglas (8.5 × 5 cm) and orientated such that a 1 mm diameter hole in each piece of Plexiglas was positioned directly over the marked region of the capsule chamber. A blunt-ended needle (0.36 mm^2 area), mounted beneath a flat weighing pan, was positioned over the Plexiglas such that the needle was perpendicular to the exposed capsule wall. Five-gram weights were sequentially loaded onto the weighing pan until the needle punctured the capsule wall. Each capsule half was punctured once. The mean puncturing force per capsule was used in all subsequent data analyses.

The second index of capsule strength measured the force needed to squeeze the plug out of intact capsules. Shore crabs (*Hemigrapsus* spp.) often ruptured *N. emarginata* egg capsules in this way by squeezing them in their chelae. Individual capsules were glued to a metal plate, which was then bolted to a vertical piece of Plexiglas mounted with strain gauges. A second metal plate was attached to a spindle so that this plate could be hand-cranked towards the mounted capsule. A chart recorder provided a record of the force required to rupture each

egg capsule. This system was calibrated with known weights.

Capsule contents. Egg capsule contents were examined to determine whether the number or size of eggs per capsule differed among populations with respect to differences in capsule structure. Eighteen freshly laid capsules were collected from each laboratory population. Each capsule was measured and then emptied of all contents. As it proved difficult to distinguish between early developing embryos and nurse eggs, no attempt was made to separate nurse eggs from embryos. Before egg counts were made, however, a few embryos from each capsule were examined to ensure that they had not advanced past the second veliger stage. At this stage, embryos are able to feed on nurse eggs (LeBoeuf, 1971; Lyons and Spight, 1973).

Egg size was also compared among sites. As egg size was relatively constant within a capsule, only five eggs were sampled from each capsule. Length and width were measured for each egg using a compound microscope equipped with an ocular micrometer. As eggs were off-round in shape, volume was estimated by using the above formula for a prolate ellipsoid.

Predation on N. emarginata *egg capsules*

Laboratory experiments. A variety of abundant intertidal organisms was collected from each field site to determine which species might prey on *N. emarginata* capsules (nemertineans: *Emplectonema gracile;* annelids: *Nereis vexillosa;* mollusks: *Mopalia* spp., *Littorina scutulata, Onchidella borealis, Searlesia dira, Tegula funebralis, Nucella emarginata;* arthropods: *Pagurus granosimanus, P. hirsutiusculus, Hemigrapsus nudus, Hemigrapsus oregonensis, Idotea wosnesenskii, Gnorimosphaeroma oregonense, Cirolana harfordi;* echinoderms: *Leptasterias hexactis, Pisaster ochraceus;* chordates: *Oligocottus maculosus, Anoplarchus purpurescens*). Groups of individuals from each species were placed in appropriately sized mesh-panelled vials (3 × 3 × 6 cm) or containers (8 × 8 × 10 cm or 20 × 20 × 10 cm), and were provided with intertidal shells or bare rocks for shelter. Containers were partially immersed in seawater tanks and provided with a continuous flow of fresh seawater. Test animals were starved for 24 h before being presented with 8 intact *N. emarginata* egg capsules. Capsules were mounted on small flat rocks using a cyano-acrylate glue and arranged in a circular configuration. A predator was defined to have opened an egg capsule only if it ruptured or ate through the chamber containing developing embryos. Capsules were checked every 1–2 days for evidence of predation, and experiments were continued for at least two weeks or until all capsules had been opened. Five to ten replicates, including controls consisting of cages with no predators, were conducted for each species.

Field censuses of predation. In May 1988, two transects (10 m in length) were established parallel to the shoreline at Grappler Inlet (48°49′55″N; 125°07′03″W) at tidal heights of 1.2 and 2.2 m above extreme low water, spring [ELWS] (Canadian datum). Quadrats (0.25 m^2) were sampled at 0.5–1.0 m intervals along these transects to determine the abundance of *N. emarginata* and their egg capsules. Egg capsules were categorized on the basis of whether the capsule chambers were intact or ruptured. The age of intact capsules was estimated by noting the developmental stage of the embryos. New capsules were identified by the presence of nurse eggs, while older capsules contained well-developed shelled embryos. Ruptured capsules were also examined to determine whether they had been attacked by predators or whether developing embryos had hatched naturally. If capsules were empty, but had been chewed into the capsule chamber, they were considered to have been opened by predators. Such capsules were described by distinctive bite marks left on the capsule walls (see Fig. 9 below). The abundance of potential predators (identified from laboratory studies) was also censused along each transect.

In June 1988, three transects were established parallel to the rocky shoreline at the Ross Islets site (48°52′12″N, 125°09′36″W) at tidal heights of 1.9, 2.3 and, 2.6 m above ELWS. The two highest transects were positioned along a steeply sloping granite wall sparsely covered with *Fucus distichus, Balanus glandula,* and *Semibalanus cariosus.* The lowest transect was set along a boulder-covered beach directly below the higher transects. Data were collected as described above for the Grappler Inlet site. A large rocky outcropping (2.8–3.1 m above ELWS) adjacent to the study site was also censused in August 1988. This 16 m^2 area was divided into six equal-sized grids and a 0.25 m^2 quadrat was thrown haphazardly into each region. Snail density, egg capsule density, and predator abundance were recorded.

Censuses of snail density or predator abundance were not made at the Seppings Island site due to its extreme exposure to wave action. Capsule remains were regularly collected, however, to compare the type of predation among sites.

Susceptibility of capsules to predators

I also conducted a series of laboratory experiments to determine whether the intertidal isopods *Idotea wosnesenskii* could differentiate between thick- and thin-walled capsules. My field observations, and also those by Emlen (1966), indicated that these were important predators of *Nucella* egg capsules. As adult isopods were able to chew through all capsules regardless of wall thickness, I chose to compare the overall preferences of these predators for thick- and thin-walled capsules.

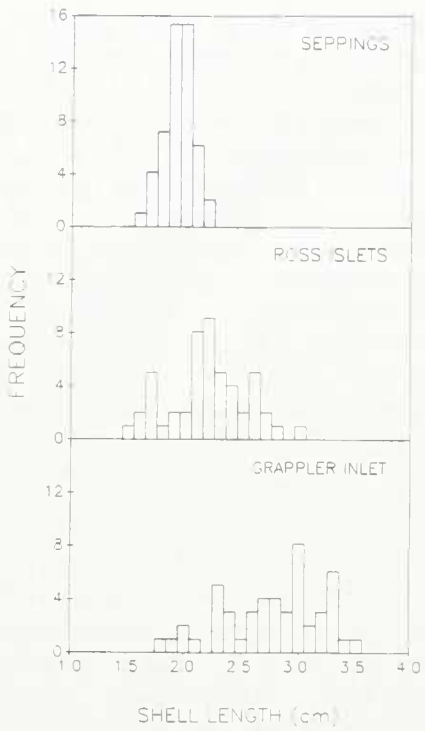

Figure 1. Size-frequency histograms of the first 50 *Nucella emarginata* individuals collected from each study site in March 1988. Snails smaller than 1.0 cm in shell-length are not included. Wave-exposure levels were predicted to be lowest at Grappler Inlet, highest at Seppings Island, and intermediate at Ross Islets. Mean shell lengths of snails are 1.9, 2.1, and 2.7 cm for Seppings, Ross Islets, and Grappler Inlet populations, respectively.

Adults of *Idotea* (mean length = 2.1 cm) were collected from Grappler Inlet in November 1988. Groups of three *Idotea* were placed in mesh-panelled cages (8 × 8 × 10 cm), and were then partially immersed in trays of fresh seawater. Predators were starved for an initial period of 24 h and then given five capsules from each of two snail populations (10 capsules in total). Predator preferences were tested for (1) thick *versus* thin-walled capsules (Grappler *vs.* Ross, and Seppings *vs.* Ross) and, (2) thick-*versus* thick-walled capsules (Grappler *vs.* Seppings). Capsules were arranged in a circular configuration, such that capsules from each population were interspersed. The number of capsules opened was recorded daily. Experiments were terminated when 4–6 out of 10 capsules had been opened. Five to ten replicate cages were used for each experimental combination.

Results

Intraspecific variation in capsule morphology

Snail size and capsule size. Snail size varied considerably among sites, with mean shell length increasing from wave-exposed to wave-sheltered shores (Fig. 1). Snail size at reproductive maturity also varied among populations. The smallest snails to spawn were 1.7, 2.1, and 2.7 cm in shell length from Seppings, Ross, and Grappler sites respectively, even though laboratory populations greatly overlapped in size (Seppings 1.4–2.2 cm; Ross: 1.4–3.0 cm; Grappler: 1.8–3.5 cm). Differences in the size of mature females within and among populations were reflected in the length of capsules produced (Fig. 2). Within each population, larger snails laid significantly longer capsules than smaller snails. Among populations, this trend was also apparent, although Seppings snails produced disproportionately large capsules per unit shell length (ANCOVA for slopes: $F = 1.20$, $P > 0.25$; ANCOVA for elevations: $F = 14.84$; $P < 0.001$). Hence, capsule size differed markedly among sites.

Micromorphology of N. emarginata *egg capsules.* Capsule walls of *N. emarginata* were composed of three laminae (L_1, L_2, and L_3; Fig. 3A,B) and were similar in structure to the capsule walls of other muricids (Sullivan and Maugel, 1984; D'Asaro, 1988). All measurements of capsule wall thickness were taken from the thick middle lamina (L_2), which consisted of a dense, fibrous middle layer (L_{2b}), sandwiched between two transparent, homogeneous layers (L_{2a} and L_{2c}). The outermost lamina (L_1) was extremely thin and often formed elaborate projections from the capsule wall. Consequently, this lamina was too difficult to measure reliably. The innermost capsule lamina (L_3) lined the capsule chamber and formed a transparent bag that enclosed developing embryos, nurse eggs, and intracapsular fluid. Sections in the apical region of the capsule indicated that this lamina was actually connected

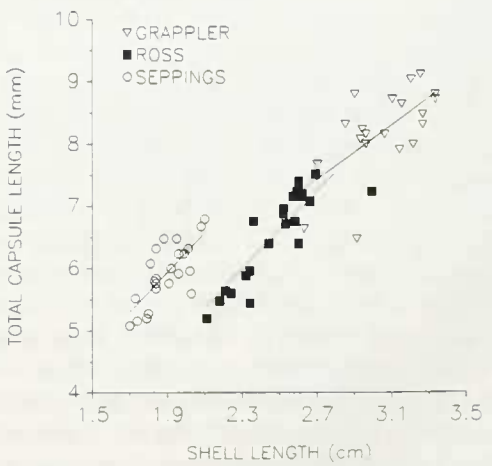

Figure 2. Relationship between total capsule length (excluding stalk) and shell length for laboratory-laid capsules from three populations of *Nucella emarginata*. Snails smaller than 1.7, 2.1, and 2.7 cm from Seppings, Ross Islets, and Grappler populations did not spawn. Least-squares linear regression equations for each site are: Seppings: $Y = 3.185X - 0.111$, $r^2 = 0.548$, $n = 23$; Ross Islets: $Y = 3.139X - 1.232$, $r^2 = 0.752$, $n = 23$; Grappler Inlet: $Y = 2.206X + 1.481$, $r^2 = 0.423$, $n = 20$.

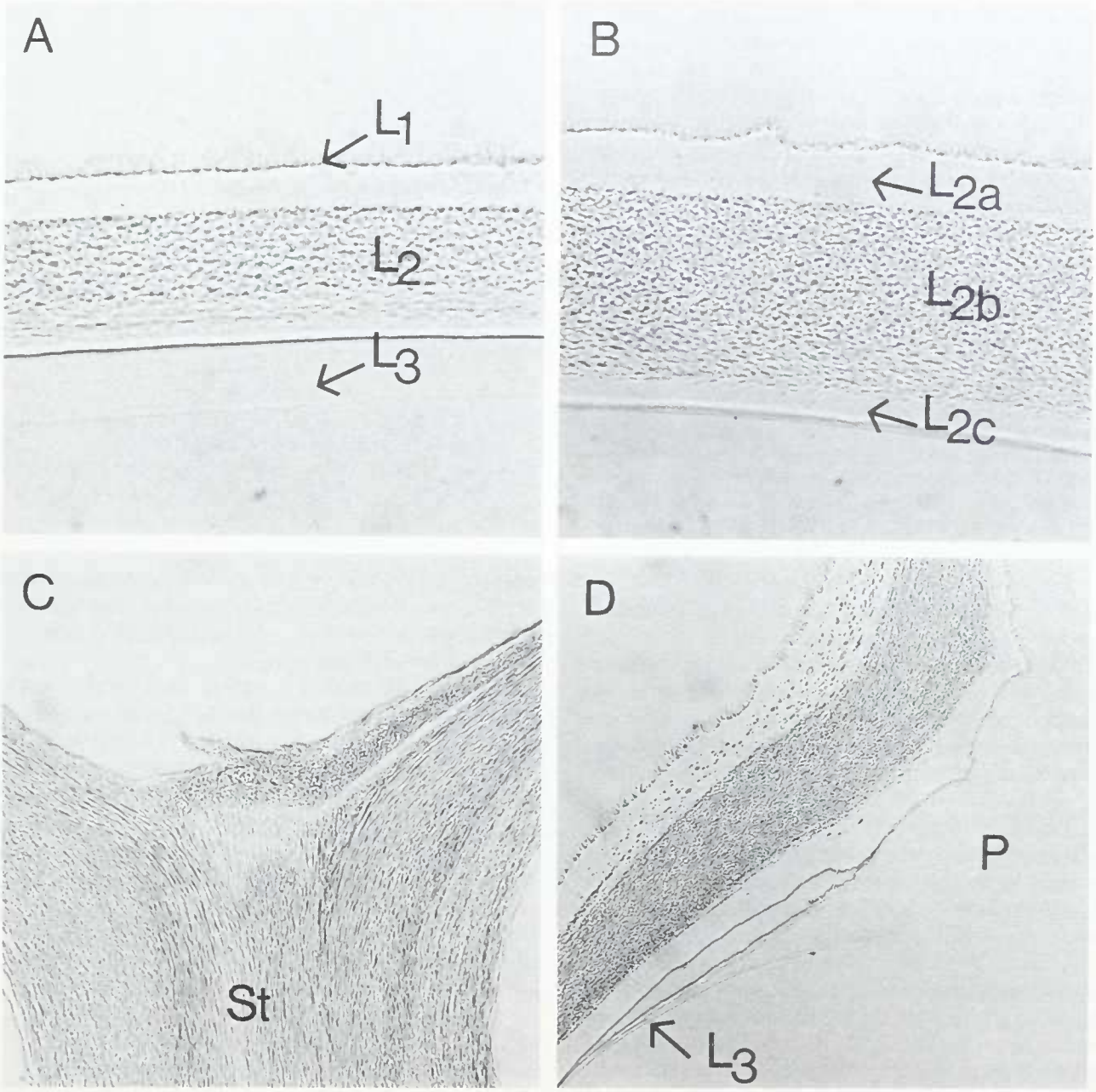

Figure 3. Microstructure of *Nucella emarginata* egg capsules: (A), (B) transverse sections taken 70% along the chamber of a capsule from Ross Islets (mean thickness = 60 μm) and Grappler Inlet (mean thickness = 90 μm), respectively; (C) longitudinal section through the capsule stalk; (D) longitudinal section through the capsule plug. Outer (L_1), middle (L_2), and inner (L_3) capsule wall laminae are indicated, as are the three component layers ($L_{2a,b,c}$) of the middle lamina, although note the disappearance of L_{2b} and L_{2c} in the vicinity of the stalk. The capsule plug (P) is also shown.

to the capsule plug and appeared to be composed of a similar material (Fig. 3D). The structure of the capsule wall was not homogeneous throughout the capsule, as is shown by longitudinal sections through the stalk and plug regions (Fig. 3C, D).

Serial sections along the chamber revealed considerable variation in capsule wall thickness (Fig. 4). Walls tended to be thickest in the plug and stalk regions and thinnest at a position 75% along the capsule chamber. Although capsule width also varied along length of the capsule

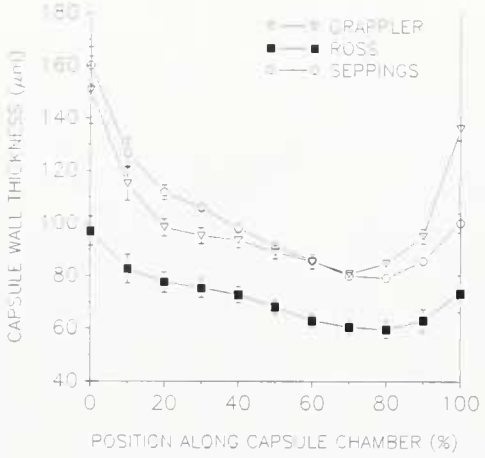

Figure 4. Variation in wall thickness along the capsule chamber of field-collected *Nucella emarginata* capsules from Grappler Inlet, Ross Islets, and Seppings Island. Serial sections were taken at 10% intervals along the capsule chamber, starting at the plug (0%) and ending at the stalk (100%). Values are expressed as mean ± 1 S.E. for 8 capsules sectioned from each population.

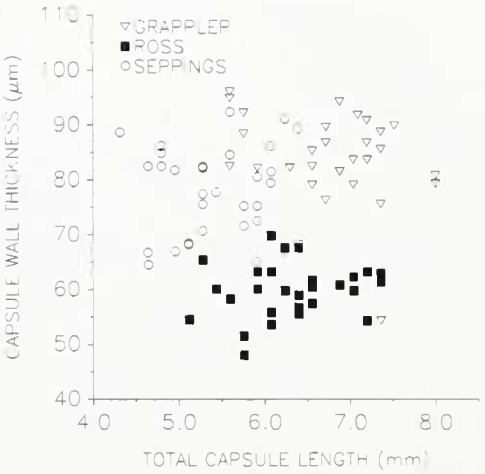

Figure 5. Variation in capsule wall thickness with total capsule length (excluding stalk) for 30 *Nucella emarginata* capsules from each laboratory population. Each value represents a mean of eight measurements taken from one section at a point 70% along the capsule chamber.

chamber, there was no correlation between capsule width and wall thickness (see Rawlings, 1989).

Capsule wall thickness also varied among populations (Fig. 4). At the 70th percentile division along the capsule chamber, Ross Islets capsules were significantly thinner than capsules from Seppings and Grappler (means of 61, 80 and 81 μm, respectively; ANOVA: $F = 29.9$, $P < 0.001$; Fig. 3A,B). This trend in wall thickness was apparent throughout the length of the capsule chamber. Differences in capsule wall thickness among populations resulted from variation in the thickness of all three component layers of the middle lamina (*i.e.*, $L_{2a,b,c}$), rather than in one component alone (data not shown).

Significant differences in capsule wall structure were also evident among laboratory-laid capsules (mean = 60, 78, and 83 μm, for Ross, Seppings, and Grappler capsules, respectively; ANOVA; $F = 81.32$, $P < 0.001$; Fig. 5). The wall thickness of these capsules did not differ significantly from capsules previously collected in the field (ANOVA; Grappler: $F = 0.54$, $P = 0.47$; Ross: $F = 0.09$, $P = 0.77$; Seppings $F = 0.29$, $P = 0.60$). Long-term exposure to the laboratory environment did not affect the morphology of capsules laid by these snails. Even after five months, snails still continued to produce their respective thick- or thin-walled capsules (data not shown).

Although the size of capsules varied extensively within and among snail populations, no relationship was evident between wall thickness and total capsule length (Fig. 5). Because capsule length was related to female shell length (Fig. 2), differences in capsule wall thickness within each population were probably not related to female size. Also, differences in capsule wall thickness among sites did not appear to reflect differences in snail size, as small Seppings snails (mean shell length = 1.9 cm) and large Grappler snails (mean shell length = 2.7 cm) both produced relatively thick-walled capsules.

Capsule wall thickness varied significantly among clutches within each population (ANOVA; Grappler, $F = 3.44$, $P = 0.02$; Ross, $F = 32.05$, $P < 0.001$; Seppings, $F = 47.52$, $P < 0.001$; Fig. 6). Variation in capsule wall thickness among clutches, however, did not obscure dif-

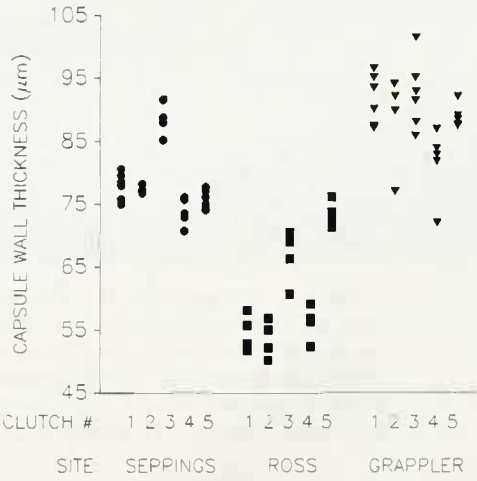

Figure 6. Variation in capsule wall thickness within and among clutches of *Nucella emarginata* capsules. Five clutches, each from a different female snail, were sampled from all three laboratory populations, with n = 6, n = 4, and n = 6 capsules/clutch for Seppings, Ross Islets, and Grappler populations, respectively. Each data point represents the mean of eight measurements taken from one section at a point 70% along the capsule chamber. Each vertical group of points represents one clutch of capsules.

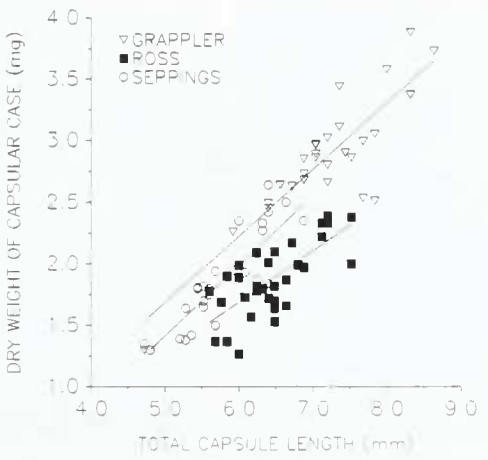

Figure 7. Dry weight of empty capsular cases as a function of total capsule length (excluding stalk) for each laboratory population. Each data point represents one capsule. Least-squares linear regression equations for each population are: Seppings: $Y = 56.859X - 142.901$, $r^2 = 0.701$, n = 27; Ross Islets, $Y = 41.359X - 79.242$, $r^2 = 0.523$, n = 33; Grappler Inlet, $Y = 53.873X - 100.746$, $r^2 = 0.740$, n = 28.

ferences in capsule wall thickness among sites. Ross Islets capsules ranged in wall thickness from 50 to 76 μm, while Seppings and Grappler capsules ranged from 71 to 92 μm and 72 to 102 μm, respectively.

Longer capsules had significantly heavier dry weights for each laboratory population of snails (Fig. 7). Although the slopes of these site-specific relationships were not significantly different (ANCOVA for slopes; $F = 1.20$, $P > 0.25$), the elevations did vary significantly (ANCOVA for elevations; $F = 50.52$; $P < 0.001$). These differences corresponded well with those in capsule wall thickness among populations, as thin-walled Ross Islets capsules weighed significantly less for a given length than thicker-walled capsules from the other two sites. Grappler capsules were also significantly heavier than Seppings capsules, again reflecting the differences reported above in wall thickness.

Capsule wall strength. The force required to puncture capsule walls differed among the three laboratory populations (Table I). Grappler capsules were significantly more resistant to puncturing than capsules from the other two sites (ANOVA, $F = 11.77$, $P < 0.001$; Tukey Multiple Comparison Test, $P < 0.05$). Ross Islets and Seppings capsules did not differ significantly in puncturing resistance (Tukey M.C.T., $P > 0.05$), despite the fact that Seppings capsules had substantially thicker walls (Fig. 5).

The force needed to rupture capsules by squeezing also varied among laboratory populations (Table I). Grappler capsules required significantly larger forces to rupture the capsular plug than did either Ross Islets or Seppings capsules (ANOVA, $F = 18.67$, $P < 0.001$; Tukey M.C.T., $P < 0.05$). Thick-walled Seppings capsules were also slightly more resistant to squeezing than thin-walled Ross Islet capsules, however, this difference was not significant (Tukey M.C.T., $P > 0.05$).

Capsule contents. No significant differences were observed in the total number of eggs allocated to Seppings, Ross Islets, and Grappler capsules (Fig. 8). Neither the slopes (ANCOVA for slopes: $F = 0.65$, $P > 0.50$) nor elevations (ANCOVA for elevations: $F = 0.36$; $P > 0.50$) of these relationships differed significantly among populations.

The size of *N. emarginata* eggs was also relatively constant. Although Ross Islets capsules contained slightly larger eggs than Grappler or Seppings capsules (mean egg volume = 40.5×10^{-4} mm^3, 39.6×10^{-4} mm^3, and 38.1×10^{-4} mm^3, respectively), these differences were not significant (ANOVA: $F = 1.55$, $P > 0.22$).

Predation on N. emarginata *egg capsules*

Laboratory-identified predators. Only three types of invertebrates opened *Nucella emarginata* egg capsules in the laboratory: isopods (*Idotea wosnesenskii*), shore crabs (*Hemigrapsus nudus* and *H. oregonensis*), and chitons (*Mopalia* spp.).

Idotea wosnesenskii regularly preyed upon egg capsules in laboratory experiments. These predators usually opened capsules by chewing through the side of the capsule chamber and left bite-marks as shown in Figure 9 (A, E).

Table I

Intraspecific variation in the wall thickness and strength of Nucella emarginata *capsules*

	Mean ± S.E.[a]					
	Grappler Inlet	(n)	Seppings island	(n)	Ross Islets	(n)[b]
Capsule wall thickness (μm)	83.3 ± 1.6	(30)	78.4 ± 1.4	(30)	59.9 ± 0.9	(30)
Puncturing force (MN/m^2)	6.18 ± 0.20	(10)	4.92 ± 0.14	(10)	5.17 ± 0.17	(15)
Popping force (N)	14.5 ± 1.0	(19)	9.7 ± 1.0	(15)	7.5 ± 0.6	(21)

[a] For each index, populations not connected by a horizontal line are significantly different from one another (Tukey M.C.T. at $\alpha = 0.05$).
[b] (n) refers to the number of capsules sampled from each population.

Caged *Idotea* (1.6–3.2 cm in body length; mean = 2.2 cm) opened a mean (± S.E.) of 4.6 ± 0.8 capsules over a five-day period (n = 11). Predation rates varied among these individuals, but not in relation to size or sex, although newly hatched *Idotea* (5 mm in length) did not open egg capsules in the laboratory. Two other species of intertidal isopods, *Gnorimosphaeroma oregonense* (mean length = 0.9 cm) and *Cirolana harfordi* (mean length = 1.4 cm), nibbled capsules extensively, but never chewed through capsule walls.

The shore crabs *Hemigrapsus nudus* and *H. oregonensis* also readily opened *N. emarginata* capsules in the laboratory. Predation rate was dependent on crab size. Small and medium-sized *H. nudus* (carapace widths of <1.5 cm and 1.5–2.5 cm, respectively) opened a mean (± S.E.) of 3.3 ± 0.8 (n = 10) and 6.0 ± 0.7 (n = 18) capsules respectively over a 5-day period. Larger crabs (carapace width > 2.5 cm) opened all eight capsules after only 3 days (n = 9). *Hemigrapsus* spp. exhibited two methods of opening *Nucella* capsules. Larger crabs typically ruptured the capsular plug by squeezing the capsule chamber in their chelae. More often, however, crabs tended to chew through the plug region directly into the capsule chamber, as shown in Figure 9(B, F).

Few *N. emarginata* capsules were opened by *Mopalia* spp. in laboratory tests. Over a 2-week period, 21 chitons only opened 6 of 56 capsules. These predators usually rasped capsules open near the base of the chamber (Fig. 9C, G), and sometimes completely severed the capsule chamber from the stalk.

Field censuses of predation. Snails and egg capsules were most abundant in the lower regions of the intertidal channel at Grappler Inlet (Table II), with egg capsules being deposited deep within a dense meshwork of mussels and barnacles. Egg capsule predators *Hemigrapsus oregonensis* (1.0–2.2 cm in carapace width), *Idotea wosnesenskii* (2.1–2.9 cm in body length) and *Mopalia* spp. (2–6 cm in body length), were present in this region, with *Mopalia* spp. being the most numerous. Eighteen percent of capsules collected along this lower transect had been opened by predators (Table II). Predators of many of these capsules could be identified by distinctive bite marks left on capsule walls (Fig. 9). The majority of capsules showed evidence of predation by *Idotea*, even though these isopods were scarce at the time of censusing. Capsules collected from three intertidal boulders showed similar types of predation, with the percentage of capsules opened by predators ranging from 11 to 26% (mean = 18%). Although there was no direct evidence of predation by *Hemigrapsus* spp. at this site, these crabs may have been responsible for opening many torn and chewed capsules whose bite marks could not be readily identified. Some capsules were also emptied by means of bevelled holes (0.4 × 0.2 mm; Fig. 9D, H). Predators of these capsules may have been intertidal gastropods, because they have been reported to make similar holes in other gastropod egg capsules (Abe, 1983).

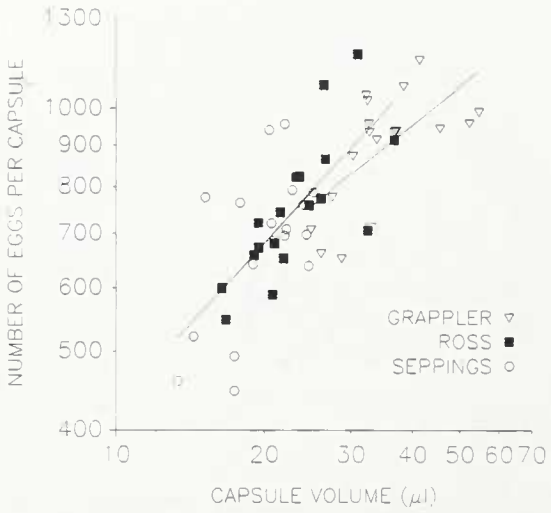

Figure 8. Relationship between the number of eggs per capsule and the volume of the capsule chamber for *Nucella emarginata* individuals from Seppings, Ross Islets, and Grappler Inlet. Counts of eggs include both developing embryos and non-developing nurse eggs. Least-squares linear regression equations for each population are: Seppings: Log Y = 0.676 Log X + 1.954, r^2 = 0.551, n = 18; Ross Islets: Log Y = 0.669 Log X + 1.962, r^2 = 0.340, n = 18; Grappler: Log Y = 0.492 Log X + 2.192, r^2 = 0.410, n = 18.

The density of snails and egg capsules was lower along the high transect at Grappler Inlet (Table II). In contrast, *Hemigrapsus* and *Idotea*, were notably more abundant, and the percentage of capsules opened was also higher, with 32% of capsules showing evidence of predation. *Idotea* bite-marks were found on all capsular remains.

Densities of snails and egg capsules varied markedly among transects at the Ross Islets site (Table II). All capsules at this site were attached to vertical surfaces or overhangs. Encapsulated embryos were also generally further developed than those at Grappler Inlet, reflecting the fact that censuses were made approximately a month later. *Hemigrapsus nudus* (0.6–2.4 cm in carapace width) were the only known predators of *Nucella* egg capsules at this site, with densities ranging up to 360/m^2. The majority of opened egg capsules also appeared to have been preyed upon by *Hemigrapsus* (Table II).

Egg capsules from Seppings Island showed evidence of bite-marks by both *Idotea* and *Hemigrapsus*. Despite the extreme levels of wave action at this site, these predators were abundant, especially within the thick beds of *Mytilus californianus*. Capsules were also found with bevelled holes identical to those collected from Grappler Inlet (Fig. 9D, H).

Susceptibility of capsules to predators

Idotea opened thin-walled capsules from Ross Islets more frequently than thick-walled capsules from either

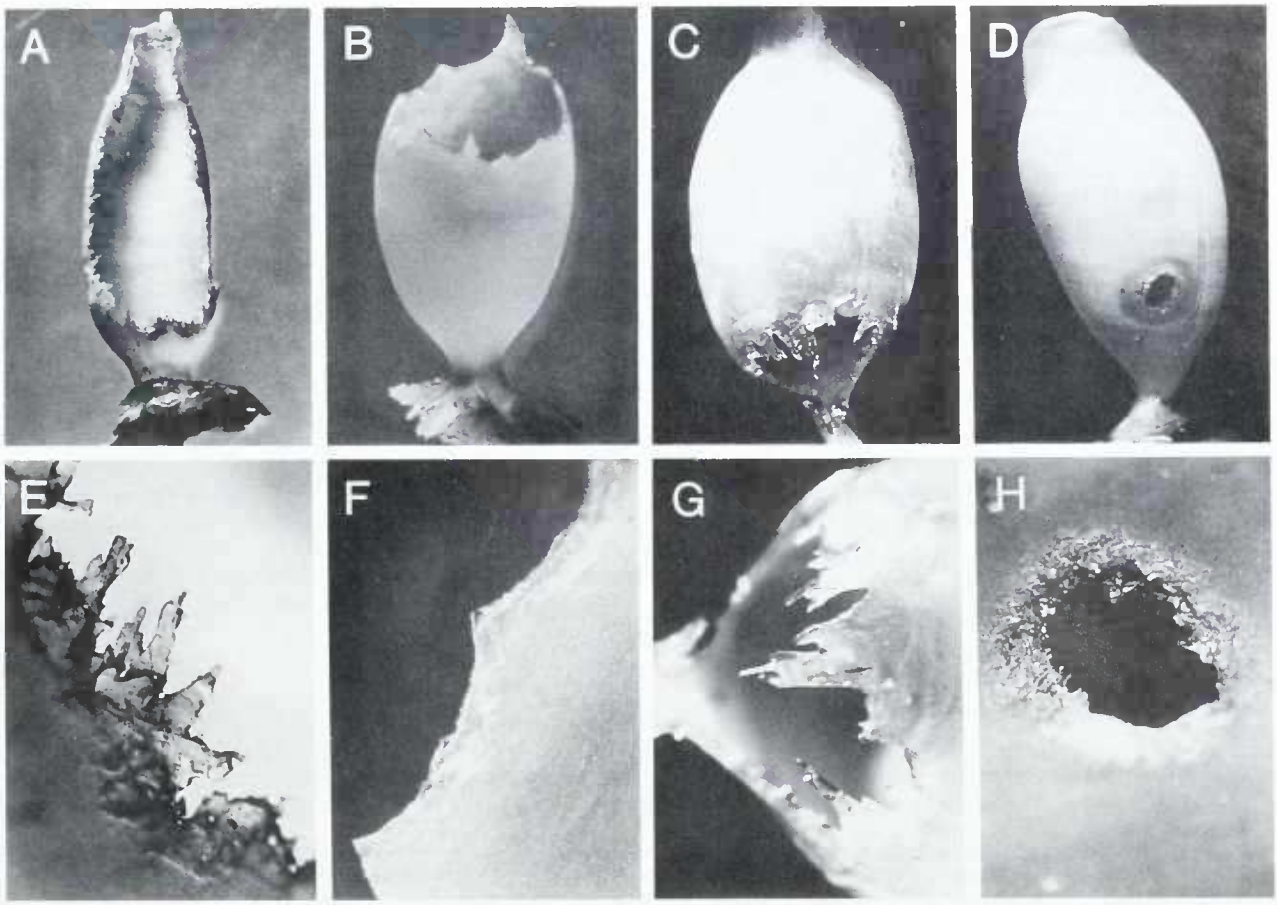

Figure 9. Characteristics of species-specific predation on *N. emarginata* egg capsules by: *Idotea wosnesenskii* (A, E), *Hemigrapsus* spp. (B, F), *Mopalia* spp. (C, G), and an unknown predator (D, H), possibly an intertidal gastropod. For each type of predator, a whole mount of the opened capsule is shown (Mag: 8X), with a close-up below illustrating the characteristic bite-marks (Mag: 25-50X).

Grappler Inlet or Seppings Island (Table IIIA, B). In 10 trials, 35 Ross Islet (thin-walled) capsules were opened compared with 15 Grappler (thick-walled) capsules (Fisher's Exact Test, $P = 0.0001$). Ross Islets (thin-walled) capsules were also opened more frequently than Seppings (thick-walled) capsules, although this difference was not quite significant (16 Ross Islets capsules *versus* 10 Seppings capsules; Fisher's Test, $P = 0.08$). In contrast, isopods did not exhibit any preferences for Seppings *versus* Grappler capsules (10 Grappler *versus* 9 Seppings capsules; Fisher's Test, $P = 0.50$; Table IIIC), and in two of six trials no capsules were eaten during a ten-day period. Hence, thick-walled capsules from Grappler Inlet and Seppings Island were more resistant to predation than thin-walled capsules from Ross Islets.

Discussion

Intraspecific variation in capsule morphology

The morphology of *N. emarginata* capsules varies extensively among populations. In the present study, both capsule wall thickness and strength differed significantly among the three intertidal locations examined. Such variation in capsular structure may reflect (1) physical constraints associated with female body size, (2) phenotypic differences in response to variable environmental conditions, or (3) genetic divergence caused by selection.

Intraspecific differences in the wall thickness and strength of *N. emarginata* capsules may reflect constraints associated with female size. Although the morphology of neogastropod egg capsules is governed by the size of the capsule gland, which, in turn, is restricted by female shell-length (Spight *et al.*, 1974; Spight and Emlen, 1976; Perron and Corpuz, 1982; present study), little is known about the direct effect of female size on capsule wall structure. Perron and Corpuz (1982) reported that wall thickness and strength of *Conus pennaceus* capsules increased with capsule size and snail shell-length. Their results suggested that the structure of capsule walls may be limited by the size of the capsule gland. In the present study, capsule size and snail shell-length varied markedly within and

Table II

Summary of Nucella emarginata *egg capsules, and potential egg capsule predators censused along transects at Grappler Inlet and Ross Islets study sites*

	Density[a] (Mean/m² ± S.E.)					Census of egg capsules[b]									
							Chamber intact		Chamber ruptured		Predators of opened capsules[c]				
	Nucella emarginata	Egg capsules	*Hemigrapsus* spp.	*Idotea* spp.	*Mopalia* spp.	# of capsules	Early embryos	Late embryos	Hatched naturally	Opened by predators	H	I	M	U.G.	UNID
Grappler Inlet															
Tidal height															
1.2 m															
(n = 8)	29.6 ± 8.8	126.0 ± 47.6	4.9 ± 0.5	0.4 ± 0.4	9.3 ± 2.1	255	35	22	22	18	4	43	2	17	34
						494[d]	24	50	0	18	3	82	0	1	14
2.0 m															
(n = 8)	14.0 ± 6.0	9.6 ± 5.2	10.2 ± 3.1	8.0 ± 3.7	0	19	68	0	0	32	0	100	0	0	0
Ross Islets															
Tidal height															
1.9 m															
(n = 6)	26.0 ± 10.4	24.8 ± 19.2	360.8 ± 38.6	0	0	37	46	5	24	24	100	0	0	0	0
2.3 m															
(n = 8)	6.4 ± 4.4	70.0 ± 30.4	0	0	0	140	19	13	45	22	77	0	0	0	23
2.6 m															
(n = 8)	289.6 ± 97.6	5.2 ± 4.8	0	0	0	10	10	0	0	0	0	0	0	0	0
2.8–3.1 m															
(n = 6)	203.3 ± 30.3	744.6 ± 17.2	24.6 ± 6.4	0	0	1117	0	7	70	22	73	0	0	0	26

[a] Censuses were made in May 1988 and June 1988 for Grappler Inlet and Ross Islet study sites, respectively. The number (n) of 0.25 m² quadrats used to estimate these densities is shown for each transect.

[b] Intact capsules were aged by examining the developmental stages of enclosed embryos. Empty capsules were categorized according to whether embryos had hatched naturally or had been opened by predators. Data are expressed as a percentage of the total number of capsules along each transect that were found in each category. Percentages may not always add up to 100%, because some capsules were found intact but their contents were dead.

[c] Predators responsible for opening capsules were identified by means of bite-marks left on the capsule chamber. Abbreviations: H = *Hemigrapsus* spp., I = *Idotea* spp., M = *Mopalia* spp., U.G. = unknown gastropod, and UNID = unidentified predators. Capsules in the "UNID" category had been opened by predators, but bite-marks could not be accurately identified. Data in each category represent a percentage of the total number of capsules opened by predators along each transect.

[d] These capsules were collected in Aug 1988 from three intertidal boulders in Grappler Inlet.

among the Grappler, Ross Islets, and Seppings populations. Capsule wall thickness, however, did not differ as predicted with either capsule length or snail shell-length. Hence, variation in the thickness of capsule walls among *N. emarginata* populations was not the result of allometric contraints associated with female size.

Differences in capsule structure among populations of *N. emarginata* also did not appear to be the result of phenotypic plasticity. Variation in capsule wall thickness within a clutch was low compared to variation among clutches produced by different individuals. Hence, within a spawning period, individual females deposited capsules of relatively consistent wall thickness. Also, snails continued to produce their respective thick- or thin-walled capsules even after five months in the laboratory, a period during which snails from all three populations were kept under similar environmental conditions. Thus, differences in the structure of egg capsules were not likely to be short-term phenotypic responses to site differences in diet, food abundance, or levels of environmental stress. Such results suggest that the production of thick or thin capsule walls may be an adaptive response to environmental conditions.

Costs associated with producing thick-walled capsules

There are likely to be both costs and benefits associated with the production of thick-walled capsules. Thick-walled capsules may incur a greater energetic cost than thin-walled capsules based on their greater dry weight per unit length. For instance, thin-walled capsular cases from the Ross Islets (6.5 mm in length) weighed 24% less than thick-walled capsules from Grappler Inlet, and 16% less than thick-walled capsules from Seppings Island. As capsular cases can account for more than 50% of the dry weight of intact capsules (*i.e.*, including the eggs; Roller and Stickle, 1988; Rawlings, unpub. data), and as *N. emarginata* capsular material has almost the same energy content per unit weight as the eggs (22.6 KJ per ash-free gram compared to 25.1 KJ per ash-free gram of embryos; J. Davis, unpub. class project, Friday Harbor Laboratories, 1984),

Table III

Preferences of Idotea wosnesenskii *for thick- or thin-walled egg capsules of* Nucella emarginata

Site Comparisons	Mean (±S.E.) number of capsules opened[a]	
	Thin-walled	Thick-walled
A) Ross *vs.* Grappler	3.5 ± 0.3	—
(n = 10)	—	1.5 ± 0.3
B) Ross *vs.* Seppings	3.2 ± 0.4	—
(n = 5)	—	2.0 ± 0.5
C) Grappler *vs.* Seppings	—	2.5 ± 0.3
(n = 6)[b]	—	2.3 ± 0.3

[a] Average number of egg capsules opened by *I. wosnesenskii* when given a choice of capsules from two different study sites. Predators were placed in cages with 10 capsules (5 from each site), and the first 5 capsules to be opened were recorded. Data are expressed as the mean number (±1 S.E.) of capsules selected from each site, where (n) refers to the number of replicates performed for each comparison.

[b] In 2 out of 6 replicates, no capsules were eaten over a 10-day period.

the energy spent in producing thicker capsule walls must represent either a substantial decrease in the energy available for egg production or an increase in the reproductive effort of an individual. In fact, Perron (1982) found that the production of thick, puncture-resistant, capsule walls among *Conus* spp. was associated with a higher annual reproductive effort than the production of weak, thin-walled capsules. In the present study, I did not compare reproductive effort among populations. The production of thick-walled capsules, however, was not associated with a reduction in egg size or number of eggs contained per unit capsule volume. Hence, on a per capsule basis, there was no evidence of a tradeoff between the amount of energy invested in capsular cases versus eggs.

Other potential costs still remain to be tested. For instance, Strathmann and Chaffee (1984) have suggested that thick encapsulating structures may reduce the availability of nutrients and oxygen to developing embryos. Hence, (1) the density of embryos per capsule, (2) the developmental rate of embryos, or (3) the proportion of embryos surviving, may differ between thick- and thin-walled capsules. Although preliminary results have indicated that there are no significant differences between the number of embryos contained within thick- and thin-walled capsules (Rawlings, 1989), further comparisons still need to be made.

Benefits of enclosing eggs within thick-walled capsules

Numerous studies have examined interspecific differences in the properties of gastropod egg capsules (Perron, 1981; Perron and Corpuz, 1982; Pechenik, 1983, D'Asaro, 1988). The degree to which thick-walled capsules protect developing embryos better than thin-walled capsules, however, is still unclear. Pechenik (1983), for example, found that the rate of salt movement across the walls of *Nucella lamellosa, N. lapillus,* and *N. lima* capsules did not vary systematically with capsule wall thickness. Hence, the resistance of capsule walls to osmotic shock or desiccation stress might not differ between thick- or thin-walled structures. Such interspecific comparisons may be confounded by differences in the structural components of capsule walls, however, which vary considerably among *Nucella* species (pers. obs.).

The only previous evidence to support the hypothesis that strong, thick-walled capsules are more protective than weak, thin-walled capsules has come from positive correlations between capsule strength, the proportion of reproductive energy invested in capsule walls, and developmental time of encapsulated embryos among *Conus* species (Perron, 1981; Perron and Corpuz, 1982). Although capsule wall thickness was not compared among all species, *Conus pennaceus,* with encapsulated development times of 26 days, was found to have significantly thicker capsule walls than *Conus rattus,* with encapsulated development times of 11 days (Perron and Corpuz, 1982). These results indicate that strong, thick-walled capsules may reflect selection for increased protection of embryos when exposure to environmental stresses is long. As yet, however, no selective mechanism has been identified to explain this pattern.

Perron (1981) has suggested that egg capsule predators may be the agent of selection for strong, energetically expensive capsule walls. Indeed, predation appears to be an important source of mortality among encapsulated embryos. For instance, Brenchley (1982) found that 52% of the capsules of the mud snail, *Ilyanassa obsoleta,* were opened by crabs or snails during 10 days of a development period lasting up to 3 weeks. Spight (1972) noted that predators had opened 77% of *Nucella lamellosa* capsules in some spawning aggregations. Other studies, such as those by MacKenzie (1961), Haydock (1964), Emlen (1966), and Abe (1983), have also documented high levels of predation on gastropod egg capsules. In the present study, one-time field censuses of predation on *N. emarginata* egg capsules indicated that up to 32% of capsules had been opened by crabs, isopods, and other predators. Therefore, predators are responsible for considerable mortality among encapsulated embryos.

Thick-walled capsules may be more difficult to open or require longer handling times by predators than thin-walled capsules. Hence, the former might be selected for in areas where predators are abundant. The production of thick-walled *N. emarginata* egg capsules was not related to the relative abundance of *Hemigrapsus* spp. among

Grappler Inlet, Seppings, and Ross Islet study sites. In fact, thin-walled capsules were found at Ross Islets, where crabs densities reached up to 360/m^2. In contrast, the predatory isopod *Idotea wosenesenskii* was found only at the two sites where thick-walled capsules were present. Embryos contained within thick-walled capsules were also less likely to be eaten by *Idotea* than those contained within thin-walled capsules. Hence, these results indicate not only that thick capsule walls protect developing embryos better against *Idotea* than thin capsule walls, but also that these predators may have resulted in selection for thick-walled capsules at Grappler Inlet and Seppings Island study sites.

Although capsule wall thickness varied in accordance with the presence of *Idotea*, capsule strength did not. The fidelity with which puncture-resistance and squeezing forces—my measures of capsule strength—simulate methods used by *Idotea* to open capsules is not known. Possibly, however, these measures of capsule strength could reflect the action of other environmental stresses affecting encapsulated embryos. Desiccation (Feare, 1970; Spight, 1977; Pechenik, 1978), osmotic stress (Pechenik, 1982; 1983; Hawkins and Hutchinson, 1988), wave-action (Perron, 1981), bacterial attack (Lord, 1986), and thermal stress (Spight, 1977; Pechenik, 1986) are all potentially important sources of mortality for encapsulated embryos. These stresses may have independently resulted in the selection of different properties of capsule walls.

Confounding influences in intraspecific comparisons

Although intraspecific variation in capsule morphology may provide the best opportunity to address costs and benefits of encapsulation, interpretations of differences among populations may be confounded by the effects of environmental stresses on adult snails. Environmental stresses, such as wave-exposure, affect the reproductive effort of gastropods profoundly. For instance, wave-exposed snails typically mature at smaller sizes and exhibit higher reproductive efforts over shorter lifespans than longer-lived, wave-sheltered snails (Roberts and Hughes, 1980; Calow, 1981; Etter, 1989). Similarly, *N. emarginata* from Seppings matured at smaller sizes and produced proportionally larger capsules than those from Grappler Inlet (Fig. 2). How such differences in reproductive effort might be reflected in the partitioning of energy between eggs and extraembryonic products is unclear. Nevertheless, the type of capsule produced should still depend on the relation between energetic cost and the defensive effectiveness of capsular material.

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